Trends in Ecology & Evolution

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Review

Gut Microbiotas and Host Evolution: Scaling Up Symbiosis

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Our understanding of species evolution is undergoing restructuring. It is well accepted that host–symbiont coevolution is responsible for fundamental aspects of biology. However, the emerging importance of plant- and animal-associated microbiotas to their hosts suggests a scale of coevolutionary interactions many-fold greater than previously considered. This review builds on current understanding of symbionts and their contributions to host evolution to evaluate recent data demonstrating similar contributions of gut microbiotas. It further considers a multilayered model for microbiota to account for emerging themes in host–microbiota interactions. Drawing on the structure of bacterial genomes, this model distinguishes between a host-adapted core microbiota, and a flexible, environmentally modulated microbial pool, differing in constraints on their maintenance and in their contributions to host adaptation.

Trends

Gut microbiotas expand current notions on how symbionts shape host evolution.

The hologenome model proposes that the host genome and its microbiome combined make a unit of evolution jointly undergoing selection.

To account for emerging themes in host–microbiota interactions, a multilayered model distinguishes between a host-adapted core microbiota and an environmentally modulated flexible microbial pool, and a range of intermediates in between

Contributions of gut microbes to host adaptation reflect this multilayered model.

Evolution in the Age of the Microbiome

The effects of microbes on animal evolution have long been recognized. J.B.S. Haldane suggested as early as 1932 that pathogens were agents of natural selection [1]. van Valen's ‘Red Queen’ hypothesis provided a mechanistic explanation, proposing that evolution is driven by the need to catch up with a continuously changing environment and, in particular, with rapidly evolving microbes [2]. Host interactions with pathogens are now thought to underlie features as fundamental to evolution as balancing selection and the maintenance of sexual reproduction [3]. While pathogens may drive evolution with a stick, mutualistic symbionts can achieve similar feats by offering the carrot. Mutualists are facilitators of niche adaptation and are thought to have prominent roles in host speciation [4,5].

While examples of species evolution driven by specific pathogens or mutualists are numerous, the full picture is likely more complex, as animals (and plants) harbor complex communities comprising diverse microbes, some more adapted to their host, others generalists, or transient, representing a broad spectrum of potential contributions. In animals, the most extensive microbiota is that of the gut. The human gut microbiota is estimated to include 10^{14} bacteria, with approximately 1000 species-level operational taxonomic units (OTUs) per individual [6,7]. Smaller organisms also harbor diverse communities: the *Caenorhabditis elegans* gut microbiota was found to include 832 genus-level OTUs, with 32 of these present in all worm populations, and the termite hindgut was reported to harbor 216 different phylotypes [8,9]. Thus, the potential diversity of host–symbiont interactions in the gut alone is immense.

Gut symbionts are often referred to as commensals and, in any given condition, some gut residents may indeed be just so; however, overall, host–microbiota interactions describe a mutualistic symbiosis. Gut microbial communities are important for diverse host functions, including development, fecundity, metabolism, immunity, and even behavior, contributing to

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both host health and fitness [10–14]. For microbes, animal intestines represent a favorable niche, as indicated by the microbial density in the human colon, which is higher than that recorded in any other microbial habitat [15]. Thus, themes identified in the contributions of specific mutualists to host evolution should be useful in evaluating those of the gut microbiota. However, the complexity of gut microbiotas could expand on these themes.

The gut microbiome (the collection of microbial genomes) offers increased genetic variation compared with the host genome, faster evolution, and the ability to exchange microbes (and their genes and associated functions) with the environment, features that could contribute to host adaptation. To address this potential, the 'hologenome' model considers the genomes of the host and its microbes as one unit under selection [16,17]. Starting with the observation that all animals (or plants) host diverse symbionts, the model proposes that symbionts can be inherited, as well as be exchanged with the environment; that association between host and symbiont affects the fitness of both; and that variation in the hologenome can be brought about by changes in either the host or the microbiota genomes. Since the inception of the hologenome hypothesis, the study of animal microbiotas has advanced considerably, generating interest in the significance of the hologenome idea for evolution, as well as criticism [18–20].

In this review, I consider contributions of the gut microbiota to host evolution as revealed by recent studies, drawing parallels to themes identified in the contributions of specific mutualists, and examining potential manifestations of the hologenome concept in such contributions. I further consider the hologenome in light of studies examining the shaping of microbiota composition, which support a multilayered structure for the gut microbiota. This structure reflects different levels of association with the host, different modes of trans-generational transmission, and different contributions to host evolution.

The Relatively Known: How Mutualists Affect Host Evolution

Speciation is a defining process in evolution: the splitting of a population into two reproducibly incompatible populations, each taking a distinct evolutionary path. Speciation is initiated by the fragmentation of a population, and isolation of the subpopulations one from another. Modes of isolation vary, including ecological isolation, behavioral isolation, developmental asynchronization, or genetic divergence, all associated with reproductive isolation, which is by definition a prerequisite of speciation. Mutualists can drive all modes of isolation, but, as facilitators of niche adaptation, they are frequently associated with ecological isolation [4].

Aphids, sap-feeding insects, demonstrate several of the central themes in the contributions of mutualists to host evolution. Plant sap is rich in carbohydrates, but poor in amino acids. In occupying this niche, aphids have become dependent on obligate bacterial endosymbionts of the genus *Buchnera* [21]. *Buchnera* provide essential amino acids in return for a stable, nutrient-rich niche in specialized bacteria-packed cells called 'bacteriocytes'. The aphid host and its *Buchnera* symbiont are mutually dependent, and their fitness is linked. To maintain symbiosis in subsequent generations, vertical transmission of symbionts from parent to progeny is favored. As a means to this end, bacteriocytes interface with aphid ovarioles, enabling direct transfer of symbionts to maturing eggs or embryos, while shielding the symbiont from the outside world [21]. The resulting fitness alignment obliges co-speciation, resulting in phylogenetic congruence between aphid hosts and *Buchnera* symbionts [22].

While the obligate symbionts of aphids are essential for host growth and reproduction, a suite of facultative symbionts facilitates more nuanced adaptations, including protection from local parasites, adaptation to particular plants or to environmental conditions, and coloration [23,24]. An individual host can harbor one or more types of facultative symbionts with varying